

## FIRE SEASON AND MULCH REDUCTION IN A CALIFORNIA GRASSLAND: A COMPARISON OF RESTORATION STRATEGIES

MARC D. MEYER<sup>1</sup> AND PAULA M. SCHIFFMAN

Department of Biology and Center for the Study of Biodiversity,  
California State University, Northridge, CA 91330-8303

### ABSTRACT

Prescribed burning and mulch reduction via grazing are two restoration strategies employed for the enhancement of native flora in California grasslands. However, the effectiveness of these methods to restore native species and suppress alien species is poorly understood. In particular, the effectiveness of different seasons of burning to restore native vegetation has been attributed to several factors, including plant phenology patterns (phenology hypothesis), fire intensities (intensity hypothesis), and accumulated mulch biomass (mulch hypothesis). In order to test these hypotheses and compare the efficacy of burning and grazing as restoration tools, the short-term effects of fire season and mulch reduction on grassland vegetation were evaluated in the Carrizo Plain Natural Area (San Luis Obispo Co., CA). Warm-season (late-spring and fall) burning significantly increased the cover and diversity of native vegetation and decreased the cover and seed viability of alien grasses relative to control treatments. Winter burning and mulch reduction did not increase the cover or diversity of native plants and were only moderately effective at reducing alien plant cover. Seed germination data showed that the seeds of one common native plant species, *Phacelia ciliata* Benth, responded positively to fire. These results indicated that fire season is a significant factor in grassland restoration, and that the success of different fire seasons for restoration is determined by plant phenology patterns, season-specific fire intensities, and potentially the removal of all mulch biomass. Warm-season prescribed burning and not grazing or cool-season burning is the most effective strategy for restoring native annual vegetation to California grasslands.

Fire is an important restoration tool for ecologists, yet very few studies have examined the significance of fire season for the regeneration of plant communities. Controlled burning programs allow resource managers to simultaneously reduce undesirable species and enhance desirable species (Towne and Owensby 1984; Parsons and Stohlgren 1989; Whisenant and Ursek 1990; Howe 1995). Such a shift in community composition may be achieved by burning strategies that incorporate the effects of fire season. These management strategies have proven to be particularly effective in the restoration of a variety of native grassland communities, including California bunchgrass (Menke 1992), Texas wintergrass (Whisenant et al. 1984), North American fescue (Grilz and Romo 1994), Kansas tallgrass prairie (Towne and Owensby 1984), Wisconsin tallgrass prairie (Howe 1995), and California valley grassland (Parsons and Stohlgren 1989).

California's valley grassland is an example of an annual dominated community in which fire is a natural and regular phenomenon (Parsons 1981). Although historic accounts of species composition are sparse, it is believed that native winter annuals once dominated this community in the relatively arid central and southern part of the state (Wester 1981; Keeley 1990). Today, however, these grasslands are

dominated by a variety of introduced annual grasses primarily of Mediterranean origin (Heady 1977; Heady et al. 1992; Keeley 1990). Most of these alien annuals are tolerant of grazing and drought, and are highly competitive (Heady 1977; Heady et al. 1992; Keeley 1990). Furthermore, they produce large amounts of mulch that suppress the growth of native plants (Heady 1956; Bartolome 1979). Most of these alien grass species in California are susceptible to fire and lack any adaptations to frequent burning (Evans and Young 1970; Smith 1970; Menke 1989). Burning reduces the aboveground biomass of alien grasses, and promotes growth of native and alien forbs (Hervey 1949; Larson and Duncan 1982; Menke 1989). However, most of these post-fire changes are transitory: Two years after a fire, alien grasses regain dominance, mulch biomass returns to pre-burn levels, and native forbs revert to a state of rarity (Hervey 1949; Bentley and Fenner 1958; Parsons and Stohlgren 1989).

Several controlled burning strategies have emerged within recent years for the enhancement of native plants in grasslands. One strategy focuses on plant phenology patterns to maximize the effects of burning. When undesirable species are more vulnerable and desirable species are less susceptible to the negative effects of fire, a controlled burn may enhance native plants or reduce exotics. Such a burning strategy has been effective in enhancing the biomass of native species in California (Parsons and Stohlgren 1989) and under-represented "phenological guilds" elsewhere (Howe 1994, 1995). In

<sup>1</sup> Present address: Graduate Group in Ecology, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616-8751.

California grasslands, carefully-timed burns have been moderately successful in the restoration of native perennial bunchgrass communities (Ahmed 1983; Keeley 1990; Menke 1992), and may be a beneficial strategy for the enhancement of native annual communities. For instance, during the late spring, alien grass seeds in California grasslands are still contained in the inflorescence and have undeveloped seed coats, making them extremely vulnerable to fire (McKell et al. 1962; Menke 1992). Likewise, in the winter, alien grasses are in the seedling stage when they are highly susceptible to disturbance. A fire during either the late-spring or winter should be detrimental to alien grass survivorship. Unlike alien grasses, native forbs maintain a persistent soil seed bank that is relatively protected from severe environmental stresses throughout the year (Young et al. 1981; Rice 1989a). Consequently, a carefully-timed burn in the late-spring or winter could be used to facilitate the concurrent reduction of alien grasses that are in a vulnerable stage of development and enhancement of native forbs that persist as seeds in the protected soil environment.

A second burning strategy for the enhancement of native diversity focuses on the relationship between fire season and fire intensity. By employing a controlled burn of relatively high intensity, resource managers can achieve elevated levels of alien species mortality. Such high-intensity fires have been successful in reducing seed survivorship of alien grasses, such as *Taeniatherum caput-medusae* (McKell et al. 1962). Native grassland species that are adapted to intense fires, however, would likely benefit from the effects of a high temperature burn. Such is the case with California grassland forbs, which occur in high densities following intense, warm-season fires (Hervey 1949; Larson and Duncan 1982; Parsons and Stohlgren 1989). Consequently, the application of a high intensity fire may be suitable for California annual grassland restoration. Unfortunately, our understanding of the relationship between fire season and fire intensity does not extend beyond the conventional wisdom that fires during the moist winter season are of low intensity and those during the dry summer season are of high intensity.

A third burning strategy for the enhancement of native plants focuses on the removal of mulch. This approach considers the amount of mulch to be the principal factor determining changes in the floristic composition in California grasslands (Heady 1977; Heady et al. 1992). Mulch refers to all dead above-ground herbage, both that lying on the soil surface and that remaining in the canopy (Heady 1956; Heady et al. 1992). Mulch acts as an insulating layer that promotes the establishment of alien grasses and suppresses the growth of native seedlings (Evans and Young 1970; Smith 1970). In the absence of mulch, grassland composition changes to one dominated by native and alien forbs (Heady

1956, 1965). Based on these observations, previous authors have assumed that burning and grazing cause similar changes in grassland composition (Heady 1977; Heady et al. 1992). Furthermore, a burn that is timed to occur when it has the greatest capacity to reduce mulch should be the most effective for the restoration of native forbs (although such a burn would also be expected to enhance alien forbs; Hervey 1949; Heady 1972, 1977; Heady et al. 1992). However, to date, no study has directly compared the effects of fire and mulch reduction on a California annual plant community. Consequently, it is not clear to what extent the direct effects of fire (e.g., high temperatures during burning) and the indirect effects of fire (e.g., higher soil moisture depletion and soil surface temperature fluctuations following mulch reduction; Evans and Young 1970) influence composition changes in California grasslands.

The purpose of this study was to directly compare the effects of fire and grazing, and evaluate the effectiveness of different burning regimes for simultaneously reducing alien plant cover and enhancing native plant cover and diversity in a California annual grassland. Three hypotheses, each addressing a specific burning strategy, were tested. These hypotheses state that the optimal burn treatment for the restoration of native plants is (1) burning when alien grass seeds or seedlings are most susceptible to disturbance (the phenology hypothesis), (2) burning when fire temperatures attain their greatest annual intensity (the intensity hypothesis), or (3) burning when fire has the greatest capacity to remove mulch (the mulch hypothesis). The specific burn season conforming to the intensity and mulch hypotheses were determined from fire temperature and mulch biomass data, respectively. The most effective burn seasons according to the phenology hypothesis were determined from phenology patterns of California annual plants. It is important to note that these hypotheses are not mutually exclusive, and that the optimal burn season may encompass the expected predictions of two or even all three hypotheses.

#### METHODS

*Experimental site.* The study site was located at the Carrizo Plain Natural Area in San Luis Obispo County, CA, a 81,000 ha preserve in the southwest corner of the San Joaquin Valley region. It is the largest remaining fragment of valley grassland in the state. The site was on a flat part of the plain at an elevation of 595 m. The soil is clayey and seasonally dry (from April–May to October–December) and derived from Miocene marine sandstones, siltstones, and shales of the surrounding Caliente and Temblor Ranges (Reid et al. 1993). Maximum temperatures average 9°C in January and 29°C in July. Precipitation, which occurs almost exclusively as winter rain, averages about 14.5 cm annually and

varied during this study from 31.1 cm/year (1994–1995) to 14.8 cm/year (1995–1996; Buttonwillow, CA; National Oceanic and Atmospheric Administration 1996). Vegetation at the site was dominated by fast-growing winter alien annuals. 97.2% and 1.5% of the total annual vegetation cover was comprised of alien and native plants, respectively. Grass cover at the site was 90.6%, forb cover was 8.1%, and bare ground was 1.3%. The site was dominated by four alien grass species: *Bromus madritensis* L., *Hordeum murinum* L., *Avena barbata* Link, and *Avena fatua* L. (in order of abundance; nomenclature follows Hickman 1993). Other less common plant species include the alien species *Erodium cicutarium* (L.) L. Hér, *Bromus diandrus* Roth, *B. hordeaceus* L., *B. tectorum* L., *Lactuca serriola* L., and the native species *Amsinckia tessellata* A. Gray, *Monolopia lanceolata* Nutt., and *Lotus humistratus* E. Greene. Mulch, which is characteristic of grass-dominated late-successional California grasslands, constituted an additional 99.3% cover in the experimental plots. Burrowing rodents, such as *Thomomys bottae* (gophers) and *Dipodomys* spp. (Kangaroo rats) were absent from the study plots but present in adjacent areas. Like grasslands throughout the region, the site had a long history of cattle and sheep grazing and periodic dryland farming (i.e., site has been plowed; Cronise 1868; Burcham 1957; Preston 1981; Stromberg and Griffin 1996). During but not prior to the period of this study, livestock were excluded from the research site by a barbed-wire fence.

**Experimental design.** Thirty 6 × 6 m plots were arranged in a rectangular grid and surrounded by a barbed-wire fence. Each individual experimental plot was surrounded by a 2 m buffer zone that was mowed for the duration of this study (June 1995 to May 1996). Six replicate plots were randomly subjected to each of the following experimental treatments: (1) unmanipulated (control), (2) mulch reduction, (3) late-spring burn (17 June 1995), (4) fall burn (24 Sept. 1995), or (5) winter burn (9 Feb. 1996). The amount of time it took to burn each plot increased from late-spring (15–30 seconds) to fall (30–60 seconds) to winter (60–120 seconds). Fires were ignited by starting a backing fire followed by a flanking fire and finally a head fire. This fire ignition sequence was used to ensure fire safety rather than for any specific experimental reason. Wind conditions during each burn were <5 mph, and each fire produced flames that were estimated to be 0.5 to 1.5 m in height. Soil surface burn temperatures were measured by placing a temperature sensitive indicator profile (Omega Engineering Inc.) on the soil surface in the center of each plot. Fall-burned plots also contained a temperature indicator profile at the plot periphery in order to evaluate the variability in fire temperature within plots. Each temperature profile contained sixteen waxes with a range of melting points (ranging from 107°C to

427°C) that were pasted on a 20 × 20 cm ceramic tile. Mulch reduction plots were mowed with an Echo weedeater and the mulch canopy was removed with a hand rake and by hand on 30 September 1995. This treatment was done to simulate the effects of grazing on mulch biomass. Care was taken not to rake the soil surface and the bottom several centimeters of the mulch canopy was left in place in order to avoid removing seeds from the soil surface seed bank. In addition, the basal 6 cm of the mulch canopy was not removed in order to minimize disturbance to this seed bank.

**Vegetation Sampling.** Vegetation in the experimental plots was sampled once in April 1995 for pre-treatment data and once in April 1996 for post-treatment data. A single post-treatment sampling period appeared sufficient to capture the short-term effects of each treatment on above ground vegetation, since: (1) previous authors have shown the effects of fire and mulch reduction to occur primarily in the first post-burn or post-mulch reduction year in California grassland (Heady 1956; Parsons and Stohlgren 1989), and (2) our visual survey of the treatment plots in the second post-treatment growing season (using a Daubenmire [1959] cover class system and pooling species according to the following groups: alien grasses, aliens forbs, native forbs), revealed that grasses had regained dominance and native forbs had become rare (<5% cover). The point-intercept method was used for both censuses, and estimates of percent cover for each plant species and species diversity of native plants were determined (Barbour et al. 1987; Schiffman 1994; Sawyer and Keeler-Wolf 1995). For the pre-treatment census, three 6 m long parallel transects were randomly positioned along an east-west axis within each plot. Pins were placed at 20 cm intervals along each transect (Schiffman 1994) and the plant species (or bare ground) encountered at each pin point were recorded (for a total of 90 sample points per plot). *Avena barbata* and *A. fatua* were lumped because of their delayed phenology and the difficulty in distinguishing them from one another given only vegetative characters. In the post-treatment census, eleven 6 m parallel transects were systematically placed along an east-west axis within each plot. Pins were placed at 50 cm intervals along this transect and data were recorded in the same manner as in the pre-treatment census (121 total sample points per plot). Analyses of variance of the pre-treatment data revealed that there were no significant differences among plots in terms of the percent cover of any plant species encountered ( $F_{1,4} > 7.71$ ,  $P > 0.05$  for each species), with the exception of *Amsinckia tessellata* ( $F_{1,4} = 14.26$ ,  $P = 0.002$ ), which was rarely encountered in either census. In order to estimate the relative biomass of mulch among treatments, the height of the mulch canopy was sampled in April 1996 in ten randomly selected locations within each plot.

*Seed bank and seed viability tests.* Ten soil samples were collected for seed bank assessment from randomly selected points within 5 control plots (collected on 30 September 1995), 6 late-spring burn plots (collected on 24 September 1995), and 6 fall burn plots (collected on 9 December 1995). Burned plot seed samples were collected following burn treatments, and all seed samples were collected prior to winter rainfall. Cores of dry soil (6 cm in diameter and 5 cm in depth) were extracted using a cylindrical bulb planter and transported to the laboratory where they were stored in plastic bags for 3–12 weeks at room temperature. The soil samples were then thoroughly mixed with vermiculite (1:1 soil-to-vermiculite ratio), placed in 5 cm diameter plastic pots in a greenhouse, and watered for a period of 4–6 weeks. All germinating forb seedlings were identified to species when possible. All germinating grasses were lumped into a single grass category.

Soil surface seed samples were collected from locations adjacent to each soil coring point within the control, late-spring, and fall burned plots. These samples were used to estimate seed viability of the soil surface seed bank following each treatment; samples were not used to estimate seed rain. Seed samples were gathered by hand at the same time that soil seed bank samples were collected, placed in plastic bags, and stored in the laboratory at room temperature for a period of 3–12 weeks. Seeds of *Bromus madritensis*, *Hordeum murinum*, *Avena barbata* and *Avena fatua*. (the four most abundant plant taxa in the Spring of 1995) were separated from the rest of the mulch material and placed on moist filter paper in petri dishes. *Avena* spp. were combined since identification to species was not possible. Each petri dish contained 10–20 seeds, and all dishes were kept moist for the duration of the seed viability study. The total number of tested seeds varied among the three grass species due to variability in sample seed densities. *Bromus madritensis* seed viability trials consisted of twenty seeds per plot, times six replicates. *Hordeum murinum* seed viability trials consisted of 100 seeds per plot, times six replicates. *Avena* seed viability trials consisted of 20 seeds per plot times three to five replicate plots. The petri dishes containing these seeds were placed in a growth chamber set at a constant 20°C and a 12-hour light/dark cycle. In addition, since *Avena* spp. are known to exhibit extended seed dormancy (Richardson 1979), petri dishes containing *Avena* seeds were treated with 5 ml of  $10^{-3}$  M gibberellic acid ( $GA_3$ ) solution to ensure radicle emergence of viable seeds (Richardson 1979). Seeds of all three taxa were scored as viable if they exhibited radicle emergence within a 20-day period.

Seed samples of the native forbs *Phacelia ciliata*, *Monolopia lanceolata*, and *Amsinckia tessellata* were also collected from experimental plots (June 1996), placed in plastic bags, and stored in the lab-

oratory at room temperature for five months. One-hundred seeds of each native species collected were subjected either to an open flame from an alcohol lamp for approximately 0.5 seconds (flame treatment) or were unmanipulated (control treatment). Seeds were then put in petri dishes (10 seeds per dish) between two moist pieces of filter paper, placed in a growth chamber set at 20°C and a 12-hour light/dark cycle, and observed for radicle emergence for a 20 day period.

*Data analysis.* Cover percentages were calculated for all major species (frequency of each species in 121 sampling points) encountered in the 1996 vegetation census. In addition, percent cover data for grasses versus forbs and native versus alien plants were determined by pooling species belonging to each of these categories. Species diversity estimates were calculated using a modified Shannon index of diversity ( $H' = -\sum P_i \ln(P_i + 0.0001)$ ; Magurran 1988). This index yielded nearly identical results as the standard Shannon index and was necessary to compensate for zero values of diversity encountered in samples lacking species in the native or alien plant guilds. Soil surface temperatures during burning were estimated using the median melting point temperature between the highest melted and lowest unmelted indicator values from each temperature profile. Percent cover, species diversity, litter height, seed viability, seed bank, and soil surface burn temperature data were analyzed with Model I one-way ANOVA. All multiple pairwise comparisons were analyzed using a Tukey's HSD test with a Bonferroni adjusted  $\alpha$  (Rice 1989b). ANOVA assumptions of randomness, independence, and normality were generally shown to be met. The ANOVA assumption of equality of variances was assessed using the  $F_{\max}$  test for homoscedasticity. In cases where this last assumption was not met, the nonparametric analog of ANOVA, the Kruskal-Wallis test, was used to compare experimental treatments. In the native seed flame-treatment experiments, a  $\chi^2$  test was used to test if seed germination was significantly enhanced by fire (for each species, samples were pooled among pretreatment plots). Differences were considered to be significant at  $\alpha = 0.05$ . All statistical tests were conducted using SYSTAT version 5.2.

## RESULTS

*Fire intensities.* Fire intensities differed significantly among the three burn seasons ( $F_{1,4} = 69.97$ ,  $P < 0.001$ ) (Fig. 1). In particular, the winter burn was significantly lower in intensity than the late-spring or fall burns. Fall burning yielded the highest soil surface burn temperatures, but these temperatures were not significantly different than late-spring burned plots. In addition, coefficients of variation for soil surface burn temperatures within a burned plot and among burned plots were similar (CV = 9.9 and 12.2, respectively).

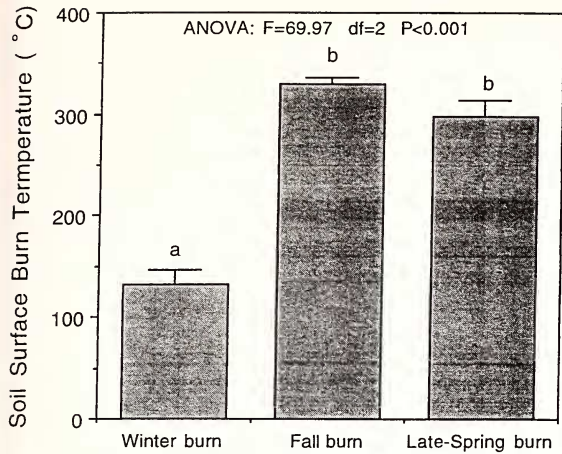


FIG. 1. Mean fire temperature (+SE) for winter, fall, and late-spring burns. Different lowercase letters indicate significant differences between treatments in this and following figures ( $n = 6$  per treatment).

*General patterns of post-fire vegetation cover.*

The percent cover of alien annual plants was significantly greater in the control plots than in the burned plots (Fig. 2a). Mulch reduction plots were intermediate with respect to alien plant cover. Among the three burn treatments, alien plant cover was highest in the winter burned plots and lowest in the late-spring and fall burned plots. In contrast to the alien cover data, the percent cover and diversity of native plants were significantly lower in the control, mulch reduction, and winter burn treatments ( $H_{1,4} = 21.47$ ,  $P < 0.001$  for native cover;  $H_{1,4} = 23.05$ ,  $P < 0.001$  for native diversity). Fall and late-spring burn treatments had the greatest cover and diversity of native plants, one order of magnitude greater than the control, mulch reduction, or winter burned plots (Fig. 2b and 3, for cover and diversity, respectively).

Both the grass and forb guilds responded strongly to the fire and mulch reduction treatments. Alien grass cover (Fig. 4a) was similar to the cover of all alien plants (Fig. 2a) in treatment plots. It was highest in the control plots, intermediate in the mulch reduction plots, and lowest in the burned plots. Moreover, among burn treatments, grass cover was lowest in the late-spring burn treatment, intermediate in the fall burn treatment, and greatest in the winter burned plots. Interestingly, patterns of forb cover (Fig. 4b) were not similar to the patterns of native plant cover (Fig. 2b) in these experimental plots. Instead, the cover of forbs was greatest in late-spring and control plots, and lowest in the mulch reduction, winter burned, and fall burned plots.

*Species cover.* The native annual forbs *Monolopia lanceolata* and *Phacelia ciliata* had significantly higher cover following the fall and late-spring burn treatments ( $H_{1,4} = 21.36$ ;  $P < 0.001$  for *M.*

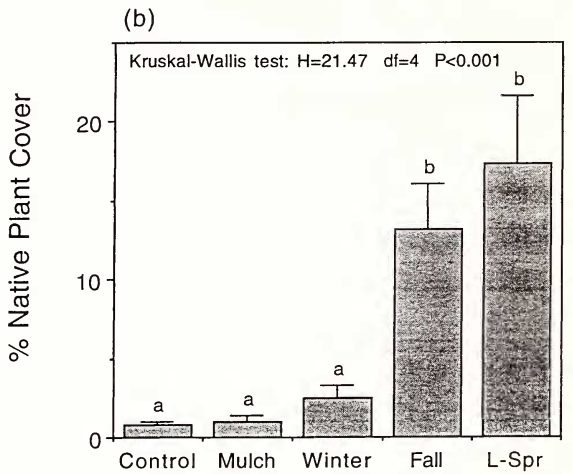
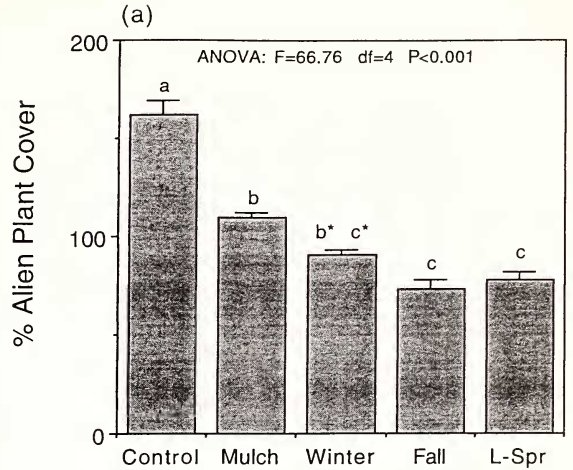


FIG. 2. Mean % alien (a) and native (b) plant cover (+SE) for the five treatments. Note that y-axis scales in these paired figures and the following paired figures are different.

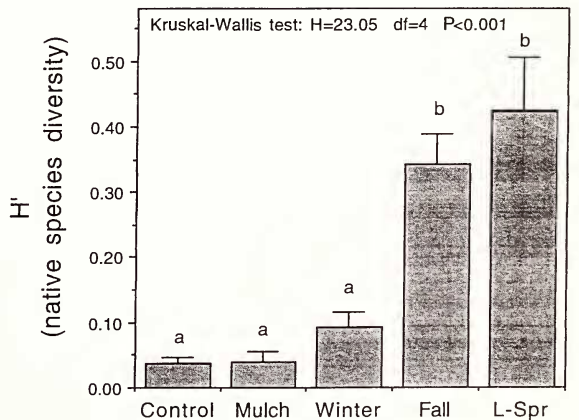


FIG. 3. Mean native plant species diversity (+SE) as indicated by a modified Shannon index of diversity ( $H'$ ).

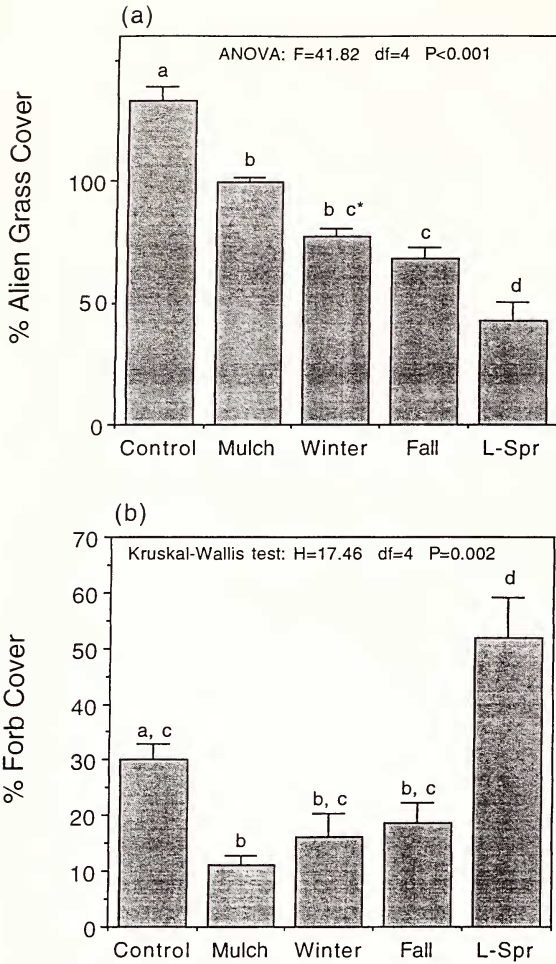


FIG. 4. Mean % alien grass (a) and forb (b) cover (+SE) for the five treatments.

*lanceolata*;  $H_{1,4} = 25.25$ ,  $P < 0.001$  for *P. ciliata*) (Fig. 5). These species were completely absent from the control and mulch reduction treatment plots and had <1% cover in the winter burned plots. Most of the native cover found in fall and late-spring burned plots (95.5% and 88.8%, respectively; Fig. 2b) was due to the combined presence of these two native forbs. Other native forbs, including *Amsinckia tessellata* and *Lotus humistratus*, had very little cover in any of the treatments. No significant treatment effect was detected for either of these uncommon native species ( $H_{1,4} = 2.20$ ,  $P = 0.699$  for *A. tessellata*;  $H_{1,4} = 5.78$ ,  $P = 0.216$  for *L. humistratus*).

Patterns of abundance of individual alien forb species were different from the trends detected for the native forb species. *Erodium cicutarium*, an alien grassland forb, had significantly greater cover in late-spring burned plots (Fig. 6a). All other treatments yielded relatively low amounts of cover for this alien forb. In contrast, the alien forb *Lactuca serriola* had the greatest cover in control plots, fol-

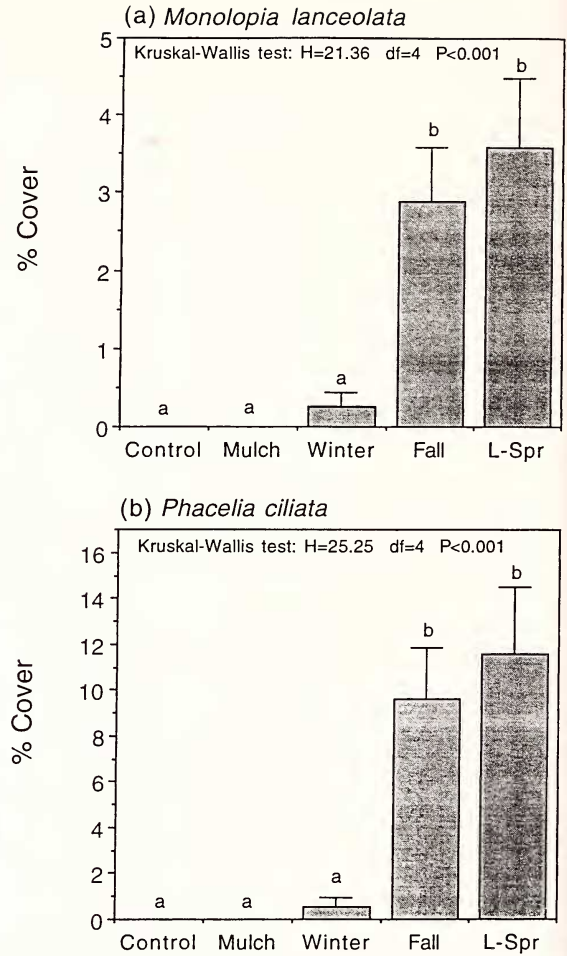


FIG. 5. Mean % cover (+SE) of the native forbs *Monolopia lanceolata* (a) and *Phacelia ciliata* (b).

lowed by the late-spring burned plots (Fig. 6b). Mulch reduction, winter burned, and fall burned plots contained relatively low cover of *L. serriola*.

Four abundant alien grass species, *Bromus madritensis*, *Hordeum murinum*, *Avena barbata*, and *Avena fatua*, collectively accounted for most of the grass cover in all treatment plots (Fig. 4a). These species tended to have their greatest cover in unburned plots, with the exception of the *Avena* spp. The cover of *B. madritensis* was lowest following winter, fall, and late-spring burn treatments (Fig. 7a). Late-spring and fall burning also significantly reduced the cover of *H. murinum* (Fig. 7b). Insignificant differences were found between experimental treatments for *Avena* spp. ( $F_{1,4} = 2.57$ ,  $P = 0.062$ ). Similarly, Bonferroni analyses revealed no significant differences ( $P > 0.05$ ) between all pairwise treatment comparisons of *Avena* spp. cover. Mulch reduction and late-spring burn treatments had the lowest cover of *Avena* spp. (Fig. 7c).

*Patterns of post-fire mulch biomass.* Burning and mulch reduction both significantly reduced the

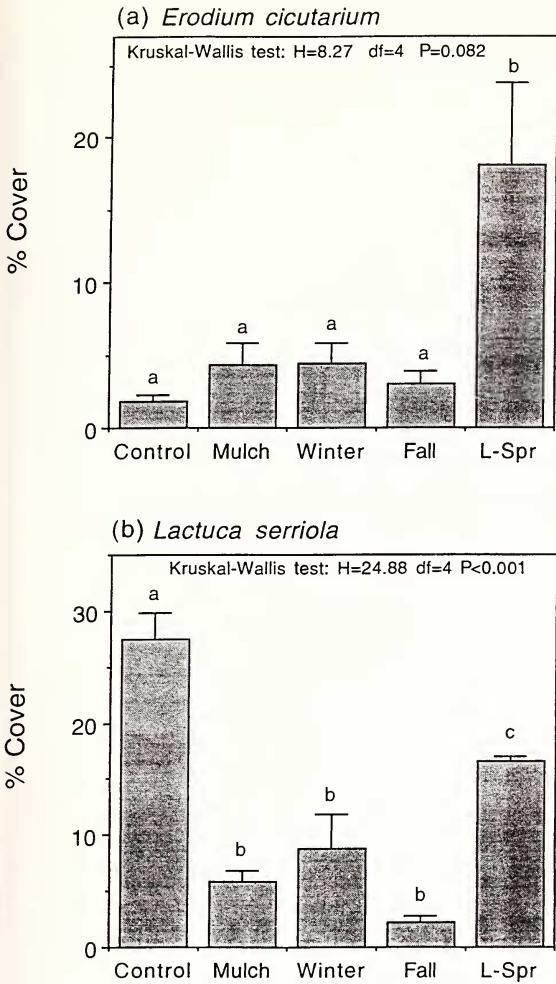


FIG. 6. Mean % cover (+SE) of the alien forbs *Erodium cicutarium* (a) and *Lactuca serriola* (b).

height of the mulch canopy ( $H_{1,4} = 23.09$ ,  $P < 0.001$ ; Fig. 8a). As would be expected, the mulch canopy was highest in the control plots. It was significantly shorter in the winter burned and mulch reduction plots, and virtually non-existent in the fall and late-spring burned plots. Bare ground was substantially greater in fall and late-spring burned plots and lower in control, mulch reduction, and winter burned plots ( $H_{1,4} = 23.14$ ,  $P < 0.001$ ; Fig. 8b).

**Seed viability and seed bank estimates.** Seed bank data complemented the vegetation data. The densities of germinating forb seeds were significantly greater in plots burned in the late-spring than those burned in the fall or left unburned (control; Fig. 9a). This high density of forb seeds in the late-spring can be attributed to the high density of *Erodium cicutarium* seeds that remained viable after the late-spring burn treatment (Fig. 9a). Germinating grass seed bank densities, on the other hand, were greatest in the control plots and lowest in the fall and late-spring burned plots (Fig. 9b).

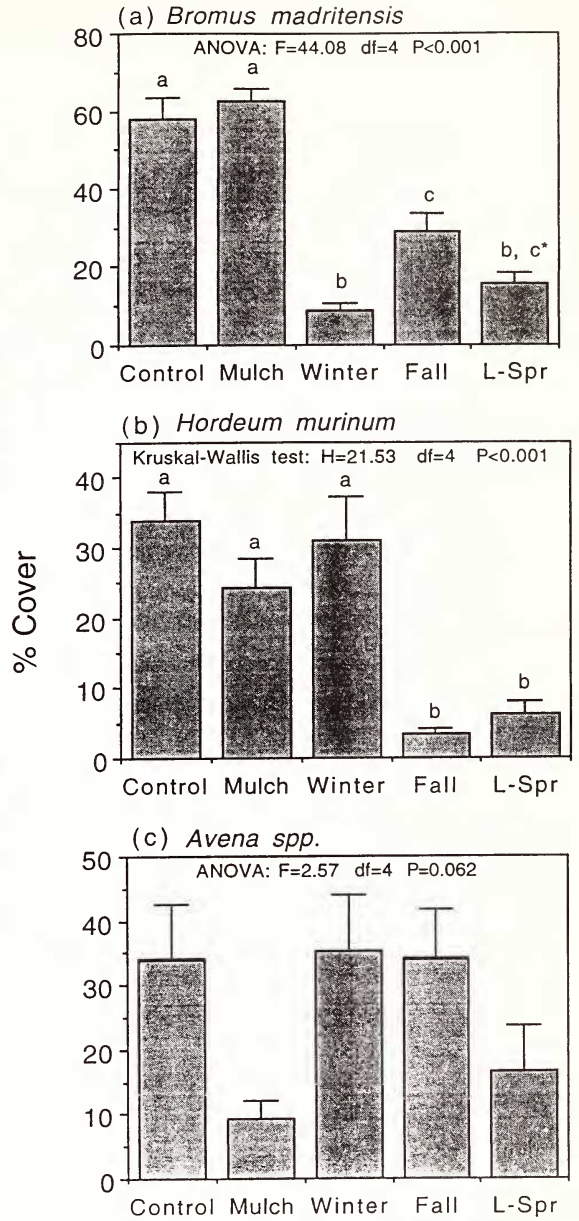


FIG. 7. Mean % cover (+SE) of the alien grasses *Bromus madritensis* (a), *Hordeum murinum* (b), and *Avena spp.* (c). For *Avena spp.*, there are no significant pairwise differences between treatments.

Seed viabilities for the alien grass taxa (*B. madritensis*, *H. murinum*, and *Avena spp.*) were highest in control plots and lowest in late-spring burned plots (Fig. 10). Although, the differences in viability between late-spring and fall burn treatments were significant for *Avena spp.* seeds, these differences were not significant for the seeds of the other two alien grass species.

In the native seed viability tests, 32% of flame-treated *Phacelia ciliata* seeds and 1% of control seeds demonstrated radicle emergence, indicating

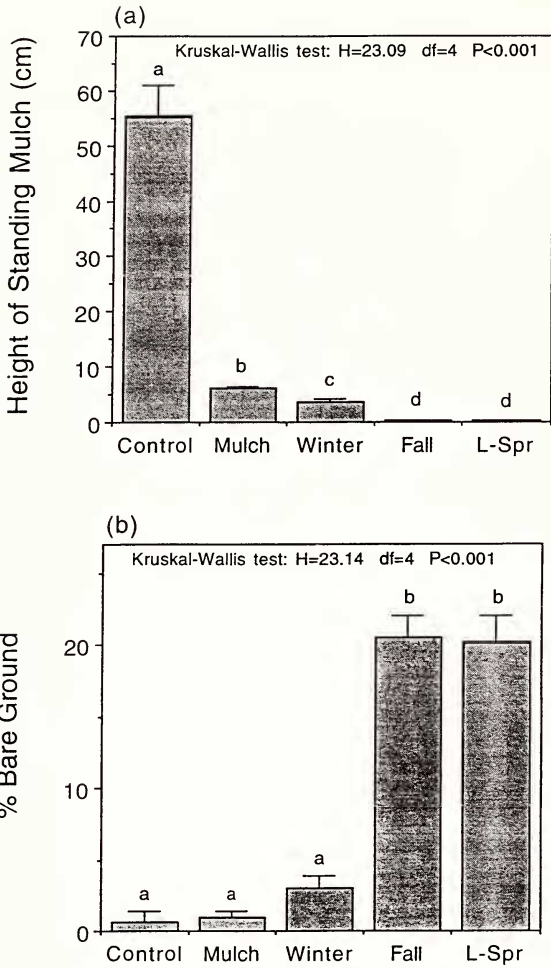


FIG. 8. Mean (+SE) height of the mulch canopy (a) and % bare ground (b) for the five treatments.

that *P. ciliata* seed germination was significantly enhanced by fire ( $\chi^2 = 34.87$ ,  $df = 1$ ,  $P < 0.001$ ). No flame-treated or control seeds of *Monolopia lanceolata* and *Amsinckia tessellata* germinated.

DISCUSSION

**Burn season restoration strategies.** Fire season has a significant influence upon the regeneration patterns of a variety of terrestrial plant communities (Martin 1983; Towne and Owensby 1984; Whisenant et al. 1984; Menke 1992; Glitzenstein et al. 1995; Howe 1995). In this study, fire season influenced short-term vegetation cover and diversity, seed viability, and fire intensity in a California annual grassland. Burn treatments also varied in their effect on native annual vegetation: warm season burns (fall and late-spring) were far more effective at increasing native species cover and diversity and at reducing the cover of alien species than cool season burns (winter). In particular, late-spring burning was most effective at enhancing native cover and

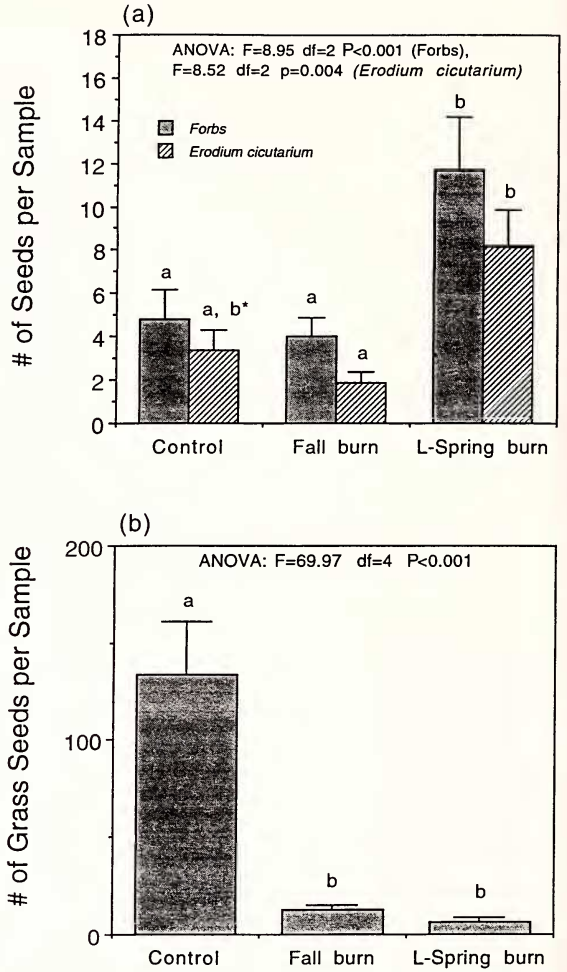


FIG. 9. Mean seed bank densities (+SE) of forbs and *Erodium cicutarium* (a) and alien grasses (b) for control, fall burn, and late-spring burn treatments.

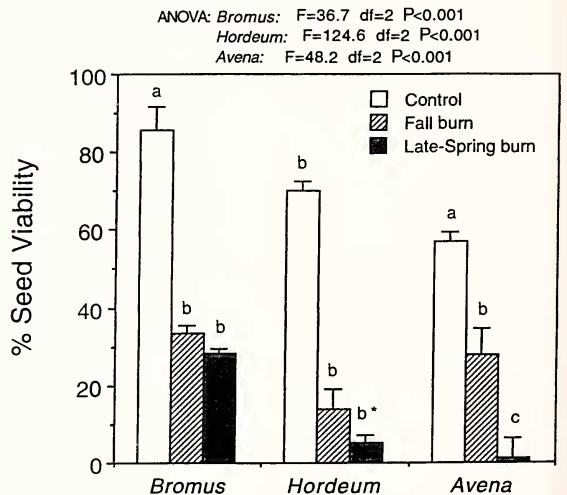


FIG. 10. Mean alien grass seed viability (+SE) for control, fall burn, and late-spring burn treatments.



reducing alien grass cover and seed viability (although it did increase the cover of *E. cicutarium*). These results indicate that fire season is an important factor for the restoration of native annuals in California. Yet, the underlying mechanism of the success of warm season burning (particularly late-spring burning) is unclear. Consequently, it is not known whether the success of warm season burning is a result of fire season and plant phenology patterns (phenology hypothesis), a fire season-intensity relationship (intensity hypothesis), or increased bare ground (mulch hypothesis). Each of these hypotheses are evaluated below.

The phenology hypothesis predicts that the most effective burn season for the restoration of native plants occurs when alien plants are most vulnerable to fire. During the winter in California grasslands, alien plants are in a vulnerable seedling stage (Chiariello 1989; Heady et al. 1992). Unlike alien grasses which lack inter-annual seed dormancy, native plants maintain a persistent seed bank in the protected soil environment (Young et al. 1981; Rice 1989a). Given these phenology patterns (particularly the greater vulnerability of alien species) it was predicted that the winter season would be an ideal time in which to burn grassland vegetation; this is assuming that substantial seed germination of alien grasses has already occurred and that fuel loads are of sufficient biomass to facilitate a fire. Native and alien plant cover data, however, did not support this prediction: winter burning was only partially effective at reducing alien cover. Moreover, it failed to increase native cover and diversity at least during the winter immediately following burning. There are three possible explanations for these results. The failure of winter burning to immediately restore native vegetation may be due to a delay in the response of native species to fire. For instance, in a previous experiment, native species such as *Monolopia lanceolata* did not show increased cover following a winter burn until the second post-fire year (P. M. Schiffman unpublished). However, based on visual surveys of all of the experimental plots (see Methods), we found no delayed effect of fire in the second year of this study. Alternatively, winter fires may not burn hot enough to induce native seed germination and cause sufficient alien plant mortality. Lastly, fire may kill germinating native seedlings along with alien seedlings, since the phenologies of these two groups are similar. Additional study of the effects of fire season will be needed to determine the plausibility these latter two possibilities.

The phenology hypothesis predicts that late-spring is also an optimal burn season for the restoration of native vegetation. In the late-spring, alien grass seeds have a high moisture content and incompletely developed seed coats and, hence, are more vulnerable to fire than later in the season when their seed coats are dry and hardened (McKell et al. 1962). Thus, based purely on plant

phenology patterns, a fire in the late-spring would be expected to have a greater negative impact upon alien grass seeds than a fire in the fall. This prediction was supported by the data: alien grass cover and seed viability were lower in late-spring burned plots. In particular, the cover and seed viability of *Bromus madritensis* and *Avena* spp. decreased significantly after the late-spring burn. These results contrasted with the previous findings of Parsons and Stohlgren (1989) who found that fall burning was more effective at reducing *Avena* and *Bromus* biomass than late-spring burning. However, this incongruence may have been due to differences in the seasonal moisture content of grass seeds between the two studies. Parsons and Stohlgren (1989) observed that alien grass seeds had a higher moisture content and were more vulnerable to fire in the fall rather than in the late-spring. If we assume that the levels of seed moisture in this study were higher in the late-spring, then this result would explain the discrepancy between the results of Parsons and Stohlgren (1989) and this study. Moreover, it would lend support to both the phenology hypothesis and McKell et al.'s (1962) seed phenology post-fire succession hypothesis.

Evidence for the intensity hypothesis was conflicting. High temperature, warm-season fires generated the greatest native species cover and diversity and lowest alien species cover. This positive association between fire intensity and native cover and negative association between fire intensity and alien cover was consistent with the intensity hypothesis. However, given that burn temperatures were generally higher or the same on fall burned plots, fire intensity alone does not explain why late-spring burning was more effective than fall burning at reducing alien grass cover and seed viability. This finding may be the result of a threshold response of alien grass seeds to elevated burn temperatures. That is, as fire intensity increases beyond some critical temperature range, it becomes an insignificant factor influencing alien grass seed mortality. For instance, seed viability in dry seeds of the California alien grasses, *Bromus hordeaceus* L. and *Taeniatherum caput-medusae*, drops dramatically at 180 to 200°C, but above and below this critical temperature range, seed viability decreases at an extremely low rate (McKell et al. 1962). The same is true of moist seeds of these two species but at a range closer to 160 to 180°C (McKell et al. 1962).

Evidence for the mulch hypothesis was also conflicting. Heady (1956) and Heady et al.'s (1992) mulch hypothesis makes two predictions: (1) the complete removal of mulch (with only bare ground remaining) should mimic the effects of fire, and (2) there is a negative linear relationship between mulch biomass and the proportion of native and exotic forb species present. The results of this study lend some support the first prediction but do not support the second. Even though 89% of the mulch

TABLE 1. PREDICTIONS AND EVALUATION OF THE THREE BURN SEASON RESTORATION HYPOTHESES. The season to the left of the greater-than sign (>) indicates the more effective burn season for native species restoration. The equality sign ( $\approx$ ) is used to signify that both treatments are similar in effectiveness. Mulch reduction refers to a significant drop in the height of the mulch canopy, whereas mulch removal refers to the removal of all mulch biomass (both in the canopy and on the soil surface).

Hypothesis	Predicted optimal burn season or result	Prediction supported?
1. Phenology hypothesis	a) winter b) late-spring	a) no b) yes
2. Intensity hypothesis	fall > late-spring > winter	yes (fall & late-spring > winter) no (late-spring > fall)
3. Mulch hypothesis	a) mulch reduction $\approx$ fall burn b) mulch removal $\approx$ fall burn	a) no b) prediction not tested

canopy was removed in the mulch reduction treatment, this treatment did not enhance native cover or diversity and was significantly less effective at reducing alien cover than the fall and late-spring burn treatments. These results may have been due to the fact that compositional changes, particularly the increase in native and alien forbs, do not occur until all the mulch canopy is removed and the ground is exposed. Thus, the greater cover of native forbs in the burned plots may be a result of the increased amount of bare ground following burning and not changes in total mulch biomass. In particular, the positive association between bare ground and native cover that was observed in this study supports this conclusion. Furthermore, bare ground has been associated with specific environmental cues that enhance germination or seedling survivorship in several annual forb species (Rice 1989a). For instance, Rice (1985) found that *Erodium botrys* (Cav.) Bertol and *Erodium brachycarpum* (Godron) Thell. had significantly higher germination on bare ground than under litter. Similarly, in the absence of dead grass blades of *Poa annua* L., emergence and survivorship of *Capsella bursa-pastoris* (L.) Medikus and *Senecio vulgaris* L. seedlings increase significantly (Bergelson 1990). Therefore, the amount of bare ground, rather than the biomass of mulch, was the more likely factor causing changes in native species cover and diversity.

Of the three burn treatments evaluated in this study, the late-spring burn prediction of the phenology hypothesis received the most support from the experimental results (Table 1). The evidence also supported the prediction that warm-season burns were more effective than cool-season burns at restoring native vegetation (intensity hypothesis). The mulch hypothesis was partially rejected based on differences in the effectiveness of mulch reduction and fire treatments for enhancing native cover and reducing alien cover.

*Responses of species and guilds.* Individual species responded differently to fire and mulch reduction treatments. The native forbs *Phacelia ciliata* and *Monolopia lanceolata* were abundant only after

a warm-season fire. Species such as these that respond positively to fire are often classified as "fire annuals" (Keeley et al. 1985). However, only *P. ciliata* appeared to be dependent on fire for significant germination: the seeds of *P. ciliata* showed a significant increase in radicle emergence following flame/heat/smoke treatment, a trait found in other species of the family Hydrophyllaceae (Keeley and Fotheringham 1998) and genus *Phacelia* (Keeley and Keeley 1982). The alien forb *Erodium cicutarium* was classified as an "opportunistic annual" (Keeley et al. 1985). Opportunistic annuals are abundant after fire but also occur in higher densities in areas where bare ground is common (i.e. canopy gaps). Moreover, unlike *P. ciliata* and *M. lanceolata*, *E. cicutarium* was common only on late-spring burn plots. The germination of *E. cicutarium* seeds was also greatest for seed bank samples collected from late-spring burned plots. Parsons and Stohlgren (1989) noted a similar increase in *Erodium botrys* density following late-spring burning, but not fall burning. Similarly, York (1997) found a decline in *Erodium brachycarpum* following a late September fire. Such a pattern may be the result of enhanced germination following exposure to the extreme temperature fluctuations of bare ground during the summer, a seed characteristic found in several species of *Erodium* (Rice 1985). *Erodium* seeds probably did not experience these wide fluctuations on fall burn plots since these plots were insulated with mulch throughout the summer. By the time of the fall burn, cooler, more moderate temperatures of the fall season predominated, and the conditions necessary for *Erodium* seed germination were lacking.

Species were also classified as mulch-dependent or fire-intolerant. The only mulch-dependent species was *Lactuca serriola*. *Lactuca serriola* cover was highest on control plots where mulch biomass was an order of magnitude or two greater than any of the treatment plots. In addition, *Bromus madritensis* and *Hordeum murinum* were considered fire-intolerant species. *Bromus madritensis* cover was significantly reduced in all burned plots, and *H. murinum* cover decreased significantly in warm-season

burned plots. Plants that exhibited none of the above patterns included *Avena* spp. and two native herbs that were uncommon in this study (*Lotus humistratus* and *Amsinckia tessellata*).

Plant guilds also varied in their response to fire and mulch reduction. Grasses were negatively affected by the removal of mulch but most significantly reduced in burned plots. Forbs, however, had greater cover in control and late-spring burned plots and lower cover in fall and winter burn plots. These post-fire patterns in forb cover contrasted with the results of Hervey (1949) and Parsons and Stohlgren (1989), who found forb cover to be consistently greater in burned plots, regardless of the season of burning. This inconsistency in forb cover can be attributed to the abundance of the alien forb, *Lactuca serriola*, in the control plots of this study. *Lactuca serriola* is common to areas of high mulch biomass in central California grasslands (M. Meyer, personal observation). However, this species was absent from the study plots of Hervey (1949) and Parsons and Stohlgren (1989). More importantly, the observation of decreased *L. serriola* cover following a fire demonstrated that not all species within the forb guild respond similarly to fire.

*Implications for grassland management.* The effects of fire on grassland composition have long been considered to be consistent with the effects of mulch reduction (Heady 1956, 1972; Heady et al. 1992). As a result, the influence of fire and livestock grazing on grassland vegetation have also been viewed as equivalent, since both methods facilitate a reduction in mulch biomass (Hervey 1949; Heady 1972). It is surprising, however, that virtually no studies directly comparing the effects of fire and mulch reduction or fire and grazing on California grassland composition have ever been conducted. Nevertheless, the direct comparison of burned and mulch reduction plots in this study strongly suggest that fire and grazing do not facilitate equivalent changes in community composition, particularly with respect to changes in native cover and diversity. This result is consistent with Stromberg and Griffin (1996) who found no increase in native species cover or diversity in grasslands recently grazed by cattle. The dissimilarity between burned and mulch reduction plots in this present study may have been the result of differences in the amount of bare ground, since warm-season burned plots had significantly more post-treatment bare ground than mulch reduction plots. Exposed bare ground following fire can cause changes in soil moisture and soil surface albedo, relative humidity, and temperature (Evans and Young 1970). Alternatively, enhanced native cover and diversity may be due to direct effects of fire. While neither of these two alternatives can be rejected with the results of this study, the latter possibility cannot be discounted for two reasons. First, alien grass seed viability was significantly reduced

following fire (a result that cannot be attributed to mulch reduction since the fall-burned seed samples were covered by a layer of mulch until they were burned). Second, radicle emergence of *Phacelia ciliata*, a species endemic to California grasslands, increased significantly following flame treatment. These results not only indicate that the direct effects of fire do have a very significant impact upon the germination and survivorship of California grassland species, but also infer that fire may have been historically important within this plant community. These results indicate that the direct effects of fire do have a significant impact upon the germination and survivorship of California grassland species. Consequently, this evidence suggests that fire is a more effective method than grazing for native species restoration.

Successful fire management in California grasslands will also require an understanding of the variable nature of plant phenology patterns within these communities. High variability in the annual rainfall in California grasslands generates high variability in the phenology patterns of grassland plants. For instance, in a dry early-rainfall year, grassland plants set seed much earlier in the season (e.g., April) than in a year of abundant, late rainfall (seeds set in June). This change in the timing of seed set with rainfall should, in turn, influence the effectiveness of a particular fire season to kill alien grass seeds and increase native plant cover. Consequently, the success of the mid-June burn in this study should not be considered to be the only date for the restoration of native biological diversity to a California annual grassland. Instead, a successful burn should be timed just prior to when alien grasses set seed, whether this occurs later or earlier in the spring season.

Fire and grazing are the primary tools for grassland management. Yet, our understanding of the efficacy of each of these strategies to restore native vegetation still remains largely unexplored. California grassland restoration and management, in particular, have long rested upon the conclusions of only a few experiments and studies that have focused almost entirely on the effects of mulch reduction (e.g., Heady 1956; Heady et al. 1965). Moreover, virtually all previous studies of California grassland vegetation have focused on the restoration of a single perennial bunchgrass species, *Nassella pulchra* (A. Hitchc.) Barkworth (e.g., Ahmed 1983; Fossom 1990; Menke 1992; Dyer and Rice 1997). This study provides a new perspective on the use of fire and grazing in California grassland management and emphasizes the influence of these management strategies on the diverse annual component of grassland communities. The conflicting results of this study with previous ones underscores the need for more comparative studies of fire, grazing, and other management practices used to restore native annual vegetation to California grasslands.

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